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Why the adaptation-selection debate is misconstrued: aDarwinian view of organizational change

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Abstract
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Keywords: organizational knowledge, organizational change, Darwin

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Why the adaptation-selection debate is misconstrued: a Darwinian view of organizational change

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Abstract: This paper is motivated by the belief that the notion of 'generalized Darwinism' offers a meta-theory that provides a logical foundation for the integration of the different theoretical perspectives in the extensive literature on the selection and adaptation of organizations. We clarify the notion of generalized Darwinism, and argue that its recursive causal logic provides the only possible explanation for the way in which organizations achieve adaptive fit. The crucial insights that can be derived from a generalization of Darwinism are twofold. First, contrary to a widely held belief, there is no logical contradiction between Darwinian and Lamarckian evolution. Second, environmental selection processes and intentional adaptation are part of one and the same process. We conclude that the explanatory logic of generalized Darwinism demonstrates that the adaptation-selection debate is misconstrued. Adaptation and selection are simply different aspects of the same evolutionary process and complement each other in a Darwinian explanation of how organizational change can lead to environmental fit.

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1. INTRODUCTION

Reviews of the extensive literature on organizational adaptation and change show that this phenomenon has been studied through a wide variety of theoretical lenses (Van de Ven and Pool 1995; Baum 1996; Lewin and Volberda 1999; Volberda and Lewin 2003). The result has been a rather fragmented theoretical landscape, and an 'adaptation-selection' debate (Baum 1996), or perhaps rather the absence of such a debate (Volberda and Lewin 2003), about the proper role of human intentionality and different levels of analysis in explanations of organizational change.

The purpose of this paper is to propose a theoretical framework that can accommodate adaptation and selection processes involving varying degrees of intentionality at multiple, interlinked, levels of analysis. This framework is derived from the tenets of 'generalized Darwinism', the notion that Darwin's (1859) theory of evolution, when properly abstracted from specific biological content, can explain the evolution of all complex, open systems. The dependent variable that is central to the adaptation-selection debate is 'adaptive fit', and this is exactly what Darwin set out to explain. We clarify the causal logic of the functional explanation that is central to Darwin's theory and demonstrate the promise of generalized Darwinism as a theoretical framework to integrate the multiple perspectives that have been brought to bear on organizational adaptation, selection and change.

In organization theory, Darwin's theory has typically been used to propose selectionist arguments at the level of a population of organizations that allow but a limited role for managerial intentionality, if at all (Aldrich and Pfeffer 1976; Hannan and Freeman 1977; Nelson and Winter 1982). However, the variation-selection-retention logic that is central to Darwinism has also been applied to selection processes within individual firms (Burgelman 1991; Baum and Singh 1994; Aldrich 1999). By unraveling the explanatory logic of Darwinism, this paper extends this work and demonstrates that the causal logic of Darwinism also applies to adaptation involving human intentionality.

The objection to the use of Darwinism in modeling organizational change has a long history and is based on the argument that the intentional behavior of human agents makes cultural evolution Lamarckian (e.g. Penrose 1952). Lamarck's theory of evolution involves directed variation and the inheritance of acquired characteristics. Directed variation means that organisms respond to changes in the environment by changes in their behavior that take account of the specific selection pressures they face. The inheritance of acquired characteristics means that adaptations acquired during the lifetime of organisms are passed on to their offspring. This is manifestly not how biological evolution works. Natural selection works with random variation and there is no inheritance of acquired characteristics, and as a result biologists have rejected Lamarckism. Yet, the human ability to learn means that cultural

evolution probably does involve the mechanisms proposed by Lamarck, and this has led many to be wary of applying evolutionary reasoning in general, and Darwinian theory in particular, to organizational phenomena. Or, alternatively, those who have applied evolutionary reasoning have typically found it necessary to state that they merely invoke it as a metaphor or a source of analogies and their theory is Lamarckian rather than Darwinian (e.g. Nelson and Winter 1982).

Yet, recent work in evolutionary economics and the philosophy of biology has shown the idea that Darwinism and Lamarckism are incompatible views of evolution to be misguided. This insight is based on the notion of generalized Darwinism: the idea that the causal structure of Darwin's theory of evolution is more than an interesting metaphor or source of analogies, but that it can, when sufficiently abstracted from specific biological content, explain the evolution of all complex, open systems. As the paper will show, the explanatory logic of Darwinism applies equally well to evolutionary processes driven by the actions of intentional agents as it does to natural selection driven by random genetic variation. The corollary of our argument is that the adaptation-selection debate is misconstrued. Both organizational adaptation and environmental selection are aspects of a Darwinian process that can involve varying degrees of human intentionality. Darwinism can thus be seen as providing a meta-theoretical foundation to integrate the different middle-range theories of organizational adaptation and selection that comprise the extensive literature on organizational learning and change.

2. GENERALIZED DARWINISM

Dawkins (1983) coined the term 'universal Darwinism' as a label for his argument that Darwin's theory of evolution by natural selection should be able to explain the evolution of any type of life that may have evolved in the universe. Since then, the term has also been used for the claim that Darwin's theory is sufficiently general to also explain evolutionary processes *within* organisms (Plotkin 1994) as well as in the cultural domain (Dennett 1995). Others prefer the term general selection to denote similar ideas (Cziko 1995; Hull et al. 2001). Here we will use the label 'generalized Darwinism' for the claim that Darwin's theory of evolution can explain the evolution of all open, complex systems. This idea is now being used to explicate the theoretical foundations of evolutionary economics (Hodgson 2001, 2002; Knudsen 2002; Stoelhorst, 2005), and can also help ground evolutionary approaches in organization studies (cf. Baum and Singh 1994).

So what, exactly, is the nature of Darwin's theory? In its most general form, a Darwinian theory of evolution involves mechanisms to introduce variations, a consistent selection process, and mechanisms for preserving and/or propagating the selected variants (Campbell 1960, 1965, 1974; Plotkin 1994). The claim of generalized Darwinism is that the explanatory structure of the variation-

selection-retention triumvirate holds across domains. In itself, the Darwinian logic is substrate neutral, and the specific mechanisms of variation, selection and retention can be expected to differ between systems. Generalized Darwinism is not itself a fully specified theory: it always requires additional middle range theories that detail the operation of the three mechanisms for the system that is being studied. In general, a Darwinian theory can therefore be understood as a specification of the variation, selection and retention mechanism for the system in question.

As Dennett (1995) has pointed out, a Darwinian explanation is in essence an algorithmic explanation: if there is a consistent selection process, and if there are mechanisms for introducing variations and retaining the favorable ones, evolution *will* occur. What has received much less attention in the applications of Darwinism in economics and organization theory is what the phrase 'evolution will occur' means. Its most basic interpretation is simply that the system in question changes over time, and this is the way in which the term is typically used by economists and management scholars. But Darwin's theory does more than explain how change can come about. It explains adaptive fit, or why systems are so remarkably well adapted to the environments in which they function. It is this feature of Darwin's theory that makes it relevant to the adaptation-selection debate.

3. DARWIN, LAMARCK AND WEISMANN

It may be clear that theories of how populations of firms change as the result of market or institutional pressures take inspiration from Darwinism, although without necessarily providing a full explication of all three Darwinian mechanisms. For instance, population ecology puts much emphasis on the selection mechanism, but the mechanism that maintains variety (organizational founding) is exogenous to the theory and the need to specify a mechanism of retention is sidestepped by assuming inertia (Hannan and Freeman 1977). In the seminal work of modern evolutionary economics, variation and retention are addressed, albeit by way of a rather problematic analogy of 'organizational routines' as the 'genes' of firms that provide stability, with a special class of 'search routines' as the source of variation (Nelson and Winter 1982).

What may not be immediately clear is that theories that emphasize the firm's ability to adapt to environmental change can also be grounded in Darwinism. There is a long history of criticism on the use of evolutionary reasoning in the cultural domain. In nature, variation is random, which is to say that it is blind to the selection pressures that organisms face. This feature has long been a reason to call organizational evolution Lamarckian (Penrose 1952; Winter 1964; Nelson and Winter 1982; Nooteboom 2000). Humans are intentional agents that can vary their behavior in ways that *do* reflect

the selection pressures they face, so that cultural evolution can be expected to involve directed variation. Moreover, cultural evolution allows the inheritance of acquired characteristics, or in other words, of adaptations that were not encoded in genes but emerged during the lifetime of an organism. This is manifestly *not* how biological evolution works, and biologists have therefore rejected Lamarckism. But they have done so in favor *not* of Darwinism *persé*, but of the Neo-Darwinian synthesis of Darwin's theory of natural selection with Mendelian population genetics. The refutation of Lamarck's theory rests on August Weismann's finding that phenotypic changes, changes in an organism's behavior and morphology during its lifetime, do not affect the genetic material that is passed on to its offspring. Weismann's barrier has become a pillar of the neo-Darwinian synthesis of Darwin's theory of natural selection with Mendelian genetics, and if we now say that cultural evolution is not Darwinian, we are really saying that it is not Weismannian (Hodgson 2001, 2002).

The logical opposition between evolution in nature and in the cultural domain is thus between Lamarckism and Weismannism. Darwinism and Lamarckism are entirely compatible. Note that the way in which we described the tenets of generalized Darwinism above does in no way invalidate its use for constructing evolutionary theories in the cultural domain, even if Lamarckian mechanisms are involved. The core of generalized Darwinism is mechanism free. Variation, selection and retention are meta-mechanisms that need to be specified to construct a full-fledged Darwinian theory. In the words of Plotkin: '*The actual mechanisms in each case*, of course – and one cannot repeat this point often enough – *are entirely different*' (1994, p.100, emphasis in original). The explanatory structure provided by Darwin is universal and holds *regardless* of the nature of variation or the mechanisms for retaining favorable variations. All that is needed is a mechanism to replenish variety, whatever its form. Whether this mechanism is blind or involves intentional action does not change the overall logic of the explanation. This is best illustrated by the fact that Darwin himself, unaware of Mendelian genetics, accepted Lamarckian inheritance (Wilkins 2001). In fact, not only is the explanatory structure of Darwin's theory and Lamarck's principles entirely compatible, on logical grounds every Lamarckian explanation needs the support of the Darwinian algorithm to work (Hodgson 2001; Knudsen, 2001).

We may thus expect adequate theories of cultural evolution to involve Lamarckian mechanisms embedded in an explanatory structure that is Darwinian. In fact, not only is the Darwinian logic still able to explain adaptive fit when intentional action leads to directed variation, such explanation only becomes easier. Consider a continuum from variation that is entirely blind to variation that is imposed by an omniscient designer. Where the actual source of variation of an evolutionary process lies on this continuum does in no way affect our ability to explain adaptive fit on the basis of the Darwinian

algorithm. In fact, Creationists have used the complexity of adaptations such as the eye as an argument for an omniscient designer ever since Paley, and the burden of proof to account for them by other means has been on the theory of natural selection. That the theory of biological evolutions has proven that adaptations can also result from a process driven by a source of variation that is on the other extreme of the continuum only shows that the nature of variation does not affect the ability of the Darwinian algorithm to explain adaptive fit. In fact, directed variation only makes adaptations more likely. If we accept that humans are boundedly rational, then the nature of variation in organizational change is likely to lie somewhere in between the extremes of the continuum. Where exactly is an empirical question, but the degree to which variation in organizational evolution is random or intentional does not change the explanatory power of Darwinism.

4. THE EXPLANATORY LOGIC OF DARWINISM

Now that we have specified what generalized Darwinism is, let us try to unravel its causal logic. The explanandum of Darwin's theory is the adaptive fit of open, complex systems. Adaptive fit is explained on the basis of an algorithm that combines variation, selection and retention mechanisms. Whether or not variation is directed doe not affect this logic. A complex system can be defined as a system that is composed of a number of interacting elements (cf. Simon 1981). Such systems necessarily involve a design that specifies the system's components and the way in which they interact. An open system can be defined as a system that requires resources from its environment to function. Such systems necessarily interact with their environments to secure the resources they need to function. Adaptive fit is the state that allows an open, complex system to function in its environment, which may require any number of specific adaptations to the system's environment.

The notion of adaptation (note that we are here referring to the noun, not the verb), is closely linked to functional explanation, which has had its share of criticism because it can easily lead to evolutionary 'just-so' stories that reek of Panglossian pan-adaptationism where 'everything is for the best in the best of all possible worlds'. A normal scientific explanation would explain a phenomenon in terms of its cause, whereas a functional explanation explains the features of a system (say, the wings of a bird) in terms of its function (flight). Vromen (1995, p.90-91) discusses the classic objection to functional explanations of the existence of a feature, which hinges on the recognition that functions are not causes but effects. A functional explanation therefore seems to reverse the logic of cause and effect: flight does not cause wings, it is having wings that makes flight possible. The problem is that wings are a sufficient, but not necessary condition for flight: there may well be functional equivalents that could have provided the same function.

Elster (1979, 1983) argues that functional explanations only work if a feedback loop can be specified that links the beneficial effect of having a feature to its prolonged existence. In biology, natural selection provides this feedback loop. It restores the logic of cause and effect by specifying how natural selection trims the set of available body plans to those that work best in the given environment. Note that this does not imply optimality, and that only the combination of natural selection with a source of variation and retention can fully explain how adaptive fit comes about over time. Without a mechanism to replenish the set of body plans in a way that provides the necessary variation for selection to act upon, adaptations would not result.

There are three necessary conditions for a functional explanation. A behavioral pattern X is explained by its function Y for system Z if and only if: [1]

Y is an effect of X;
Y is beneficial for Z;
Y maintains X by a causal feedback loop passing through Z.

The third condition needs further clarification and brings us to the distinction between genotype and phenotype. In biology the phenotype is the combination of the organism's morphology and behavioral repertoire that determines the way in which it interacts with its environment. The organism's phenotype is derived from the genotype, the genetic information that codes for the way in which the phenotype develops. The genotype both enables and constrains the organism's interaction with its environment. The distinction between genotype and phenotype is essential to the way in which the Darwinian algorithm works. Over time, there needs to be a causal feedback loop from phenotype to genotype. In biology, this causal feedback loop is provided by differences in reproductive success. The

[1] These conditions are derived from Elster (1979, p.28), who derives five conditions for a functional explanation in the social sciences. His formulation is as follows. An institution or behavioral pattern X is explained by its function Y for group Z if and only if: (1) Y is an effect of X; (2) Y is beneficial for Z; (3) Y is unintended by the actors producing X; (4) Y (or at least the causal relationship between X and Y) is unrecognized by the actors in Z; (5) Y maintains X by a causal feedback loop passing through Z. However, given the premise of generalized Darwinism, conditions 3 and 4 are superfluous. The Darwinian algorithm also works when intentionality is involved.

fact that some organisms are more successful in propagating their genes will change the composition of the genotype from one generation to the next.

The distinction between genotype and phenotype is a fundamental part of a Darwinian explanation. For the Darwinian algorithm to work, there must be way to retain information about what has worked in the past, and this information must underwrite the way in which a system interacts with its environment. It follows that we need to understand open, complex systems in terms of the way they interact with their environment, or their *behavior*, and in terms of what 'codes' for that behavior, or their *codex*.[2] This codex can be understood as the accumulated information about what has worked in the past. The notion of 'Y maintains X by a causal feedback loop passing through Z' can thus be generalized to: the relative success of different behaviors in the interaction with the environment changes the codex of the system so that the likelihood that the system displays successful behaviors increases.

The idea of a codex that underlies a system's behavior brings us to a final point about the causal logic of Darwinism that goes back to Ernst Mayr's (1961) classic paper on the concept of causation in biology. If Darwinism is about explaining adaptive fit, and if adaptive fit is about behavior that allows a system to function in its environment, then Darwinism is about explaining behavior. But there are two types of explanation of behavior in biology, which Mayr termed 'proximate' and 'ultimate'. A proximate explanation would explain an animal's behavior in terms of how the behavior occurs. Such explanations are typically cast in terms of the environmental cues that trigger a certain behavior. For instance, migratory species of birds may begin their migration because the length of daylight in a twenty-four-hour period drops below a certain value. Such explanations should be distinguished from ones that are cast in ultimate causes of behavior. Ultimate explanations are not about *how* an animal's behavior comes about, but about *why* it does. Ultimate explanations assess the adaptive value of behaviors and establish why a certain behavior may have evolved. In the case of migrating birds, their behavior may be the result of a long history of selection caused by a decline in the insect population during the autumn and winter months, which may have made migration to warmer climates with more numerous insect populations an adaptive reponse. In biology, ultimate causes concern the *encoding* of information into the genotype, whereas proximate causes deal with how *decoding* that information results in phenotypes with specific structural and functional features.

[2] We adopt this term from Wilkins (2001).

5. DARWINISM AS A META THEORY

We have seen that adaptations are properties of a system that come about through introducing variation in the traits of a system, selective pressure from the environment on these traits, and the differential propagation of those traits that confer some advantage on the system. Selection works on the way in which systems interact with their environment. The Darwinian algorithm means that if there are mechanisms for introducing variation in the system's behavior, a consistent selection process, and mechanisms for retaining those behaviors that confer an advantage to the system in its interaction with the environment, then behavioral adaptations will result. Over time, the behavior of the system is in a quite literal sense informed by its local environment.

Adaptations can thus be understood as beneficial features of a system shaped by interaction with the environment. Two features of adaptations are important. The first is their goal-directed nature. Every adaptation is 'for' something. The second is their relational quality. Every adaptation is some form of organization of the system relative to some feature of environmental order. Adaptations simply cannot be seen in isolation from the environmental factors that have provided the selection pressures for them. Plotkin (1994) convincingly argues that given these two characteristics adaptations and knowledge are essentially the same thing. '[A]ll adaptations are instances of knowledge, and human knowledge [as commonly understood] is a special kind of adaptation' (p.117). The goal-directed property of adaptations can only result if adaptations are 'in-formed' by features of the world; 'they are highly directed kinds of organization, and not random, transient structures that may or may not work. Adaptations do work, and they work precisely because of this 'in-forming' relationship between organismic organization and some aspect of the order of the world' (p.118).

The importance of this view of adaptations as knowledge of the environment is that it again shows intentionality to be secondary to the overall argument. Any adaptation constitutes knowledge of the environment, and the knowledge of conscious beings like ourselves, which may involve thought and which allows us to act intentionally, is but a special kind of knowledge. The view that knowledge as commonly understood is but a special kind of adaptation means that learning can be understood as the manifestation of a Darwinian process. In other words, learning is a process of variation, selection and retention, in which information from the environment about what works and what doesn't provides the feedback loop that is necessary for the system to become adapted.

This is not to say that there aren't subtle differences between selection and learning (cf. Vromen 1995, p.119). Selection is about changes in populations. It assumes individual stasis, and can only trim the designs of the systems (individual organisms, say, or firms) that make up the population. Learning is

about changes within systems. It leads to changes in the codex of systems that allow them to behave differently in their interaction with the environment. But over time, both processes lead to adaptive fit, and both processes need mechanisms of variation and retention to do so. In this fundamental sense, selection and learning are merely different manifestations of the same Darwinian logic.

Plotkin (1994) uses the concept of a 'Darwin machine' to underscore this point.[3] A Darwin machine is any system whose transformation over time through successive adaptive states is explained by a process of variation, selection and retention. Populations of entities without any capacity for individual learning can function as a Darwin machine, as long as selective pressure from the environment affects the differential propagation of these entities over time. This is how natural selection in biology works on populations.

There are in fact, a number of other systems that can be understood as Darwin machines and that have been described as such. These include the immune system, the brain, and the scientific enterprise (Plotkin 1994; Cziko 1995; Dennett 1995). What is particularly relevant for the adaptation-selection debate is that over the years many authors that have studied individual learning in its various guises, from operant conditioning of pigeons to the fully conscious thought involved in science, have taken to modeling it as a Darwinian process (e.g. Skinner 1981; Campbell 1974; Popper 1972). In each case, of course, the specific mechanisms of variation, selection and retention are different, but the general Darwinian logic still applies.

The tenets of generalized Darwinism suggest that if different types of individual learning can be understood as a Darwinian process, we may follow a similar route when modeling organizational learning. After all, organizations, like organisms, are open complex systems that depend on scarce resources from the environment for their survival. Modeling organizational learning as a Darwinian process that leads to behavioral adaptations would ground theories of organizational adaptation and selection in a proven explanatory logic that is especially well suited to dealing with the multi-level dynamics and recursive causalities that are involved in the processes by which organizations come to fit their environment. Moreover, understanding the way in which organizations become adapted to their environment as the result of a process of variation, selection and retention can help integrate theories that emphasize environmental selection mechanisms with those that favor explanations in terms of intentional variations in the firm's design and behavior. The Darwinian logic shows that these theories simply address different aspects of the same process.

[3] Plotkin (1994) credits William H. Calvin for the term Darwin machine.

6. ONLY DARWINISM CAN EXPLAIN ADAPTIVE FIT

The logic of generalized Darwinism discussed above shows that theories of organizational adaptation face the same task as theories of environmental selection: they need to specify how a firm behaves in relation to its environment, where the variation in its behavior comes from, and how behavior that works is retained. Organizational adaptations are what enables the firm to act upon environmental cues. More specifically, they are what underwrites the range of functional behaviors of the firm in relation to its environment. These adaptations are the accumulation of information about what has worked in the past and result from the interplay of variation, selection and retention mechanisms. These mechanisms allow the organization to vary the way in which it behaves, to test how successful different ways of interacting with the environment are in securing the scarce resources that the organization needs to survive, and to retain those behaviors that are successful.

If we assume bounded rationality, a combination of mechanisms for variation, selection and retention is not only a sufficient, but also a necessary condition for adaptations to evolve in a changing environment. The only logically consistent alternative explanation for adaptive fit is an omniscient designer. Consider the alternatives where one of the mechanisms is missing. Let us assume a population of entities. In the case of a selection and retention mechanism without a source of variation, we have a system where unsuccessful entities get weeded out and successful ones are retained.[3] This situation is akin to choosing from among a fixed stock of things and may be termed ‘subset selection’ (Knudsen 2002). In a stable environment, this may lead to an equilibrium. If we have a set of apples and, for instance, blemished apples are selected out, we may end up with a set of apples that fit a selection environment favoring unblemished apples.

But as soon as we allow the selection pressure to change over time, the explanation breaks down. When, for instance, the selection criterion changes to the color of the apples and only red apples are favored, then, assuming that there is variety in the color of the apples within the set of unblemished apples,[4] the only effect can be a further trimming of the set. In the limit, an algorithm consisting of a selection and retention mechanism without a mechanism to replenish variety can only result in an empty set. Next, consider the case of a variation and retention mechanism without selection. Here we have a situation where 'everything goes'. Every variation that comes about is retained through time because there is no selection pressure. In the limit, this algorithm can only lead to an infinite set. Finally, consider the case of a variation and selection mechanism without retention. This amounts to a system without memory. Variation is generated completely haphazardly, rather than being informed by past success. Because success in environmental interaction is purely a matter of chance, in the limit such an algorithm will result in an empty set. Moreover, an algorithm consisting of only variation and selection cannot evolve any sort of complexity. Without a feedback loop to retain information about what works, there can be no accumulation of information about what works.

It follows that, barring an omniscient designer, *only* the combination of variation, selection and retention mechanisms can explain adaptive fit. This is not to say that there cannot be organizational change in the absence of one of the three mechanisms. There can be variations that are selectively neutral and that do not positively or negatively affect the success of the firm in extracting scarce resources from the environment. But given scarcity and a changing environment the Darwinian algorithm is the only way in which a system can learn and evolve adaptations. This means that the adaptation-selection debate should be redirected from discussions about the relative importance of intentionality to discussions about what we know about the mechanisms of variation, selection and retention in and between organizations. Reframed in this way, the many theories that touch upon aspects of organizational adaptation, selection, learning, and change come into focus as middle range theories that provide rich hunting grounds for the necessary details on how the Darwinian triumvirate works for organizations.

[4] Note that this situation also leads to two logical problems with regard to the assumption of there being a population of entities to select from. First, without a source of variation, where do these different entities come from? Second, given a limited number of entities in the population and without a Darwinian history involving all three mechanisms, why would there be entities among the population that fit the environmental conditions they face? This is also the problem of population ecology theory, which its proponents solve by invoking the mechanism of organizational founding, which, however, is exogenous to the theory.

7. MIDDLE-RANGE THEORIES OF ORGANIZATIONAL CHANGE

The claim of generalized Darwinism is that its explanatory structure is sufficiently general to apply to all open, complex systems. Note that its specification above does not refer to any concepts that are specific to biology. Darwinism can thus be seen as a meta-theory that is applicable across domains. Its importance as such can hardly be overstated. So far, it is quite simply the only fully specified and logically consistent explanatory structure to account for adaptive fit that we know. At the same time, generalized Darwinism is not itself a fully specified theory and always needs to be complemented by a further specification of what the mechanisms of variation, selection and retention for the system in question are. For the case of firms, the disparate literatures that have touched upon the selection and adaptation of firms as reviewed by Lewin and Volberda (1999) offer many insights into the specific mechanisms of variation, selection and retention as they act both upon and within firms. The promise of generalized Darwinism, then, is that it offers a meta-theoretical structure that can help integrate the middle-level theories of adaptation, selection and learning that comprise organization science.

Population ecology, institutional theories, evolutionary economics, contingency theory and industrial organization all emphasize different aspects of the selection mechanisms that act upon firms. Population ecology (e.g. Hannan and Freeman 1977) and evolutionary economics (e.g. Nelson and Winter 1982) focus primarily on how the market selects efficient firms, while institutional theories (e.g. DiMaggio and Powell 1983) focus on the broader institutional context and emphasize how selective pressures emanating from norms and shared logics affect the firm's legitimacy. Industrial organization and its application to competitive strategy in Porter's (1980, 1981) five forces framework provides additional details about the sources of selection pressure in competitive markets, while contingency theory (e.g. Mintzberg 1979) puts into focus the effect of such environmental conditions as the rate of environmental change and complexity on the success of different organizational forms. In addition to these literatures, which all focus on the selection between firms, there is also work on selection within firms (e.g. Weick 1979; Burgelman 1991; Campbell 1994; Aldrich 1999).

The literatures on strategic choice, the behavioral theory of the firm, organizational learning, dynamic capabilities, and process studies of strategy have a lot to say about how variations in the behavior of firms come about. The notion of strategic choice, or the idea that organizations need not only be passive subjects of environmental selection pressures but may also have the power to reshape their environment (Child 1972, 1997) is central to that argument that managerial intentionality can play an

important role in how firms achieve adaptive fit.[5] It is also central to most of the strategy literature. On the other hand, the behavioral theory of the firm (Cyert and March 1963) and process studies of strategy (e.g. Quinn 1980) emphasize that the effects of managerial intentionality on the strategy of a firm are mediated by decision processes that involve multiple stakeholders and substantial uncertainty, so that strategies may have to satisfice on conflicting political pressures and often evolve in a piecemeal manner. The theories on organizational learning (e.g. Argyris and Schön 1978) and dynamic capabilities (e.g. Teece et al. 1997) add an emphasis on the constraints on an organization's ability to change its interaction with the environment imposed by path dependency.

Finally, retention mechanisms have an important place in many theories, although they are typically not specified in much detail. For instance, population ecology (Hannan and Freeman 1977) simply assumes inertia, while evolutionary theory (Nelson and Winter 1982) goes a step further by taking recourse to a biological analogy with the notion of routines as the genes of organizations, but does not specify how behavior becomes routinized. The nature of the codex of the firm thus emerges as perhaps the central question of a Darwinian theory of the evolution of organizations. What provides an organization with the stability that it needs to function and where is information about what has worked in the past retained so that it can direct future behavior? Where, in other words, does organizational knowledge reside? Theories of organizational learning, with their emphasis on single and double loop learning (Argyris and Schön 1978, March 1991) suggest that the codex of the firm may be multi-layered, as do theories of organizational culture (Schein 1985). And the resource-based theory of the firm, with its emphasis on competencies and capabilities may also be a good starting point to further unravel the mechanisms by which firms accumulate information that helps them to adapt to their environments.

[5] Note that this notion is entirely compatible with the Darwinian logic as developed above and has its counterpart in biology, where it comes under the heading 'niche construction'.

CONCLUSION

The aim of this paper has been to make a simple, yet fundamental point. We have shown that Darwinism offers a general logic to explain adaptive fit that is especially well suited to account for the multi-level and recursive dynamics that are involved in the processes by which firms come to fit their environment. Contrary to a widely held belief, a Darwinian explanation can also accommodate intentional behavior. In fact, unless we want to take recourse to an omniscient designer, the logic of generalized Darwinism offers the only complete and logically consistent causal explanation of how complex open systems can evolve adaptations to a changing environment. This leads to the conclusion that the adaptation-selection debate is misconstrued. To construct a complete and logically consistent explanation of why organizations fit their environment, both theories that emphasize intentional adaptation and theories that emphasize environmental selection face the same essential task of specifying all three Darwinian mechanisms and the recursive causality between them. In fact, given human agents with bounded rationality it is a logical necessity that an empirically adequate account of organizational learning combines adaptation and selection arguments. Generalized Darwinism thus provides a meta-theory that can help ground and integrate the literatures that discuss organizational adaptation and selection.

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